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Research Article

Negative impact of the invasive topmouth gudgeon (*Pseudorasbora parva*) on population growth of a native fish species, the sunbleak (*Leucaspius delineatus*)

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Abstract

Biotic interactions of invasive and native species are one of the main drivers of declining freshwater biodiversity. The recent population declines of sunbleak (*Leucaspius delineatus*) in its native range have been attributed to the spread of the rosette agent (*Sphaerothecum destruens*) carried by the invasive topmouth gudgeon (*Pseudorasbora parva*). However, both fish species highly overlap in their habitat preferences and omnivorous feeding strategy and their interspecific interactions may have contributed to the decline of sunbleak populations. To test this hypothesis, we carried out two experiments in small (0.8 m^3 water volume) and large (8 m^3 water volume) outdoor mesocosms and followed their population and individual responses over one growing season in single-species and syntopy treatments. In each experiment, both species reached similar final abundance, final biomass and biomass-based population growth rate in the single-species treatment. However, the final biomass and biomass-based population growth rate of sunbleak were much lower than those of topmouth gudgeon in the syntopy treatment in both experiments. That is, the biomass-based population growth rate of topmouth gudgeon was not affected by interspecific interactions, while that of sunbleak significantly declined. These disparate population-level responses of both species to syntopy were not reflected in the individual-level responses. At the end of each experiment, topmouth gudgeon individuals were heavier than sunbleak individuals of the same size and individuals in the large mesocosms were heavier than conspecific individuals of the same size in the small mesocosms, but we found no difference between the single-species and syntopy treatments. Taken together, these results suggest that the presence of topmouth gudgeon in the small waterbodies can significantly impact sunbleak populations. More broadly, it underscores the need to mitigate invasive species' effects on native fish through proactive conservation and management strategies.

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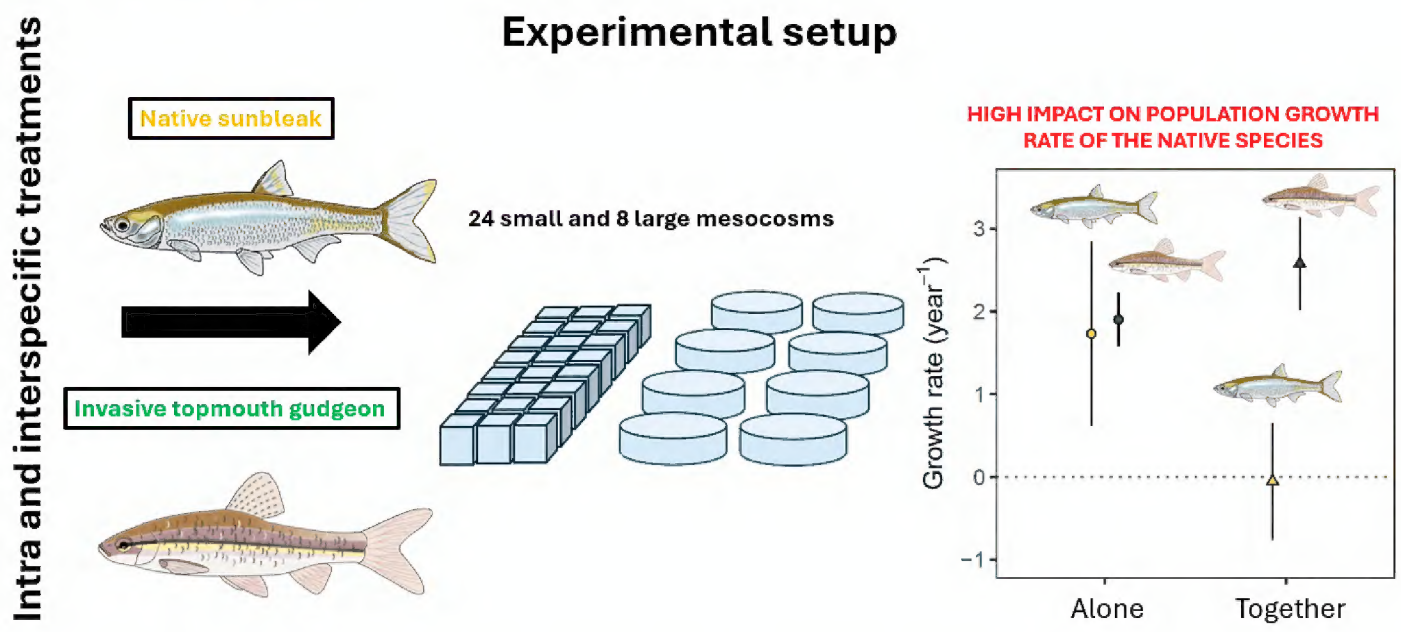
Graphical abstract



Key words: Alien species, biodiversity decline, competitive exclusion, non-native species, stone moroko, wetlands

Introduction

Invasive non-native species are one of the most dangerous threats to freshwater biodiversity (Clavero and García-Berthou 2005; Dudgeon et al. 2006; Soto et al. 2024) and can affect populations of native species through competition for resources (Tapkir et al. 2023), predation (Rechulicz and Płaska 2021), disease transmission (Andreou et al. 2011) or their combinations. Highly successful invasive species may even trigger large-scale changes in ecosystem functioning (Aloo et al. 2017; Geist et al. 2023) and contribute to the downsizing of entire food webs (Young et al. 2016; Dijoux et al. 2024).

Due to commercial importance of inland aquaculture, commercial fisheries and people´s enthusiasm in recreational angling and ornamental fish trade, many fish species were spread outside their native ranges and became invasive in the 20th century (Balon 2004; García-Berthou 2007). Some of those invasive species became very successful (van der Veer and Nentwig 2015) and ubiquitous in the invaded area, strongly reducing native species population size (Šmejkal et al. 2024a). This is well documented for some large-sized and commercially important native fish species. For instance, collapse of fisheries, based on lake trout (*Salvelinus namaycush*) in Great Lakes, led to detailed research of sea lamprey (*Petromyzon marinus*) ecology and massive control of its larvae densities in the tributaries of Great Lakes (Grunder et al. 2021). Less attention is being paid to steep population declines of small-sized fish species with low commercial value and with no direct interest of fishermen or recreational anglers (Šmejkal et al. 2025). One such species with declining populations in continental Europe is sunbleak (*Leucaspius delineatus*) (Lelek 1987; Šmejkal et al. 2025). The sunbleak was listed in the Red List of Czechia as nearly threatened in 1995, its status changed to endangered in 2003 and to critically endangered in 2010 (Chobot and Němec 2017). Although this species is currently listed as least concern under IUCN Criteria (Freyhof 2024), the populations declined to their lowest recorded levels in several EU countries (Šmejkal et al. 2025).

The decline of sunbleak populations has been attributed to the spread of the rosette agent (*Sphaerothecum destruens*) by the invasive topmouth gudgeon (*Pseudorasbora parva*) (Gozlan et al. 2005). The topmouth gudgeon is on the EU blacklist of

invasive species and well known for its significant negative impact on native biota (European Commission 2014; Kajgrová et al. 2022; Adámek et al. 2024) and is also an asymptomatic carrier of the rosette agent (Andreou et al. 2011; Ercan et al. 2015; Spikmans et al. 2020). However, not all populations of topmouth gudgeon carry the rosette agent (Spikmans et al. 2013), which suggests that interspecific interactions between the two species may contribute to the sunbleak population decline. Both fish species are small-sized (up to 10 cm), omnivorous, thriving in wetland habitats and have good tolerance for hypoxic conditions (Gozlan et al. 2010; Radtke et al. 2022). Both species also reproduce several times each year and can reach very high densities within a year after colonisation of a small waterbody (Gozlan et al. 2003, 2010).

To verify whether the interspecific interactions between sunbleak and topmouth gudgeon without the influence of the rosette agent can impact sunbleak populations, a mesocosm experiment has been designed where single-species and syntopy treatments were set in 24 small mesocosm (800 l) in a randomised complete block design. In addition, eight large mesocosms (8000 l) were inoculated with sunbleak (two), topmouth gudgeon (two) and syntopy (four) to verify small mesocosm trends in larger ecosystems. It was hypothesized that: i) the competition of the native sunbleak with the invasive topmouth gudgeon will negatively impact sunbleak population growth rates and final densities; ii) the invasive topmouth gudgeon population growth rates and densities will be affected by the competition with native sunbleak to a much lesser extent and iii) the condition of sunbleak will be more negatively impacted by interspecific competition compared to topmouth gudgeon.

Materials and methods

Fish, zooplankton and macrophyte collection and maintenance

To provide environmental conditions similar to natural habitats, zooplankton and phytoplankton inoculum and macrophytes necessary for spawning (white waterlily, *Nymphaea alba*) were collected from the fishpond Vrabce, located near České Budějovice (48°92.5521'N, 14°37.5078'E) and (48°59.9982'N, 14°22.9186'E) and transferred to separate 500 l circular vats kept outside in an open space. Macrophytes were soaked in water with 3 kg of sugar per vat overnight to avoid contamination by other organisms (snails, oligochaetes) and then transferred in clean water for rinsing. Fish were collected at Překážka Pond (sunbleak; 49.0843064°N, 14.1515947°E) and Šuspák Pond (topmouth gudgeon; 48.9806511°N, 14.4195850°E) and the populations were naïve to interspecific interaction with the other species prior the experiment.

Mesocosm experiment

The experiment was conducted in 24 small and eight large outdoor mesocosms at the Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czechia. Each of the small tanks (98 cm length × 91 cm height × 90 cm width) received 800 l of tap water and 7.5 kg of sand from the S P Bohemia, k.s., České Budějovice (Czechia). The large tanks (circular with 3 m diameter and 150 cm depth) were filled with 8000 l of tap water. One white waterlily was suspended 0.4 m below the water level in each small and large mesocosm and roots were covered in a netting with an addition of 1 kg soil from experimental area. Two litres of a well-mixed inoculum of phytoplankton and zooplankton were added to

each mesocosm on 12 April 2024. Six data loggers (HOBO Pendant Temperature/ Light 64 K Data Logger, Onset Computer Corporation, Bourne, Massachusetts, USA) were placed in three random small and large mesocosms at 0.5 m depth to continuously monitor water temperature during the experiment. The temperature ranged from 8 to 27.5 °C in small mesocosms and from 11 to 25.5 °C in large mesocosms. The average temperatures were similar with 20.5 ± 3 °C in small and 20.6 ± 2.6 °C in large mesocosms. Temperatures did not reach upper thermal limits causing mortality in these species (Radtke et al. 2022). Mesocosms were kept without fish from 12 April 2024 to 12 May 2024 to reach high invertebrate densities before fish introduction on 12 May 2024. The experiment was performed until 20 September 2024. Mesocosms were checked visually for any sunbleak mortality and 20 sunbleak from syntopy treatment were subsequently kept in the indoor aquaria for two months to ensure no disease outbreak as reported in Gozlan et al. (2005).

We introduced 10 fish per mesocosm, all of them conspecific in the two single-species treatments (sunbleak only and topmouth gudgeon only) or five individuals of each species in the syntopy treatment (in total 320 fish: 160 sunbleak, 160 topmouth gudgeon). Each fish standard length (*SL*) was measured to the nearest mm and weight in g (*W*, with precision 0.1 g). Sex was not possible to determine in most of individuals due to their small size. Total biomass density of the fish at the start of the experiment differed between treatments in the small mesocosms, but not in the large mesocosms (Suppl. material 1: fig. S1, table S1, see Statistical analyses below for details). In the small mesocosms, the total biomass density at the start of the experiment was slightly higher in the syntopy treatment (mean ± SD, total = 14.4 ± 1.3 $g.m^{-3}$; sunbleak = 7.3 ± 0.6 $g.m^{-3}$; topmouth gudgeon = 7.0 ± 0.8 $g.m^{-3}$) than in the treatments with only sunbleak (12.3 ± 0.9 $g.m^{-3}$) or topmouth gudgeon (12.8 ± 0.7 $g.m^{-3}$; Suppl. material 1: fig. S1, top row). In the large mesocosms, the differences in initial biomass densities between treatments were negligible (sunbleak only: 1.97 ± 0.04 $g.m^{-3}$; syntopy: total = 1.97 ± 0.04 $g.m^{-3}$, sunbleak = 0.97 ± 0.03 $g.m^{-3}$, topmouth gudgeon = 1.00 ± 0.10 $g.m^{-3}$; topmouth gudgeon only: 2.06 ± 0.11 $g.m^{-3}$). All introduced fish were between 25 and 62 mm of *SL*.

At the end of the experiment, the mesocosms were drained with a water pump (Karcher SP 9.000 Flat 16458100, Winnenden, Germany) and fish scooped out in the buckets with hand nets (mesh size 3 mm knot to knot, 40 cm frame, 1.2 m handle; Pokorný-sítě s.r.o., Brloh, Czechia). Fish *SL* and *W* were recorded for at least 40 individuals of each species in each mesocosm if available; all individuals were measured and weighed if their number was lower. In total, 448 individuals were measured and weighed (sunbleak: 124 in single-species treatment, 84 in syntopy; topmouth gudgeon: 121 in single-species treatment, 119 in syntopy). The remaining 3,900 individuals, predominantly small offspring, were sorted to species, counted and their total weight per mesocosm recorded.

Genetic verification of *Sphaerothecum destruens* presence in the experiment

After termination of the experiment, a random sample of 10 and 10 topmouth gudgeon from single species and syntopy treatment was taken, respectively. Similarly, 10 and 24 sunbleak were taken from single species and sympatry treatment to target eventual infection in sympatry treatments. DNA was extracted from the dissected tissue of the kidney and liver of experimental fish. Magnetic Blood DNA Extraction

Kit (Vazyme, Nanjing) was used in combination with the Automatic nucleic acids extraction instrument VNP-32YL (Vazyme, Nanjing). The protocol and the PCR primers were adopted from Mendonca and Arkush (2004). One round of PCR with primers Sd-F and Sd-1R, amplifying fragments of 18S rDNA of *Sphaerothecum destruens*, was used and checked on the gel. As a positive control, a synthetic fragment of a corresponding part of 18S rDNA of the species was used (IDT, Integrated DNA Technologies), based on NCBI available sequences (accession number AY267346), while PCR water was added as a negative control. All PCR reactions were carried out in Biometra T3000 thermocycler (Göttingen, Germany) with the following cycling conditions: 5 min at 95 °C; 30 cycles of 30 s at 94 °C, 30 s at 65 °C, 30 s at 72 °C; 7 min at 72 °C. PCR reactions were run in 30 µl of 15 µl of PPP Master mix [150 mM Tris–HCl, pH 8.8, 40 mM $(NH_4)_2SO_4$, 0.02% Tween 20, 5 mM $MgCl_2$, 400 µM dATP, 400 µM dCTP, 400 µM dGTP, 400 µM dTTP and 100 U/ml Taq-Purple DNA polymerase], 1 µl of each primer (10 pmol/µl) and 1.5 µl genomic DNA. PCR products were electrophoresed on 1.5% agarose gels.

Statistical analyses

We analysed the effects of syntopy treatment on both fish species at the individual, population and assemblage levels. At the individual level, we analysed the effects of experimental design (small vs. large mesocosms), species identity and syntopy in the experiment (i.e. whether or not both species co-occurred in the same mesocosm), as well as density dependence on fish condition using the allometric relationship:

$$\ln(W) = \ln(a) + b \ln(SL) \quad (1)$$

Density dependence was quantified by the total density of fish biomass in the respective mesocosm at the end of the experiment TW_{end} (g.m^{-3}) as a proxy for the entire duration of the experiment.

We used linear mixed models with the mesocosm identity as a random intercept to model Eq. 1. We assumed either a constant or a species-specific allometric slope $b = b_{sp}$ and combined each of these models with 10 models for the allometric intercept: (1) constant $\ln(a) = \ln(a_0)$, (2) species-specific $\ln(a) = \ln(a_{sp})$ corresponding to sunbleak ($sp = L$) or topmouth gudgeon ($sp = P$), (3) depending on the combination of species and syntopy treatment $\ln(a) = \ln(a_{ss})$, corresponding to sunbleak-only ($ss = LN$), sunbleak in syntopy ($ss = LY$), topmouth gudgeon in syntopy ($ss = PY$) and topmouth gudgeon-only ($ss = LN$), (4) density-dependent $\ln(a) = \ln(a_{DD}) = \ln(TW_{end})$, (5) depending on the mesocosm type $\ln(a) = \ln(a_{exp})$ and (6)–(10) all pairwise combinations of species (or syntopy treatment), mesocosm volume and fish biomass (Table 1).

For the population-level response, we used the final biomass density $TW_{SS,\,end}$ (g.m^{-3}) and population size $N_{SS,\,end}$ in each mesocosm (converted to population density $TN_{SS,\,end}$, ind.m^{-3}, in the figures) for each combination of species and syntopy treatment (see above for the four *ss* values; note that $TW_{SS,\,end} = TW_{end}$ in the single-species treatments). For the assemblage-level response, we used the final total biomass density TW_{end} and population density N_{end} (converted to population density TN_{end}, ind.m^{-3}, in the figures) in each mesocosm. We analysed the differences in final population state of each species in each syntopy treatment using generalised mixed linear models (GLMMs, Gamma distribution for biomass density and negative binomial distribution for population size) and random intercept to account for

Table 1. Comparison of all candidate models of the individual length-weight allometry (Eq. 1) for each species and syntopy treatment in the small and large mesocosms. Best model in bold; other plausible models with ΔAICc ≤ 2 highlighted in bold italics. Model structure: W = weight, SL = standard length, b_{sp} = species-specific slope, a_{sp} = species-specific intercept, a_{ss} = species- and syntopy-specific intercept, a_{DD} = density-dependent intercept, a_{exp} = different intercept for individuals from small and large mesocosms; all models contain the same random effect component (1 | *Tank*). df = degrees of freedom; ln(L) = log-likelihood; ΔAICc = AICc difference from the best model; w = Akaike weight based on AICc; rank = model rank.

Model	Model structure	df	ln(L)	ΔAICc	w	Rank
LW1	$\ln(W) \sim a + b \ln(SL)$	4	0.2	14.8	$< 10^{-3}$	18
LW2	$\ln(W) \sim a + b_{sp} \ln(SL)$	5	7.6	2.1	0.072	6
LW3	$\boldsymbol{\ln(W) \sim a_{sp} + b \ln(SL)}$	***5***	***7.8***	***1.7***	***0.090***	***4***
LW4	$\ln(W) \sim a_{sp} + b_{sp} \ln(SL)$	6	7.9	3.5	0.035	10
LW5	$\ln(W) \sim a_{ss} + b \ln(SL)$	7	8.8	3.7	0.033	11
LW6	$\ln(W) \sim a_{ss} + b_{sp} \ln(SL)$	8	8.9	5.7	0.012	15
LW7	$\ln(W) \sim a_{DD} + b \ln(SL)$	5	1.1	15.0	$< 10^{-3}$	20
LW8	$\ln(W) \sim a_{DD} + b_{sp} \ln(SL)$	6	8.0	3.2	0.042	8
LW9	$\ln(W) \sim a_{exp} + b \ln(SL)$	5	2.2	12.9	$< 10^{-3}$	17
LW10	$\boldsymbol{\ln(W) \sim a_{exp} + b_{sp} \ln(SL)}$	***6***	***9.4***	***0.5***	***0.163***	***2***
LW11	$\ln(W) \sim a_{sp} + a_{DD} + b \ln(SL)$	6	8.2	2.8	0.051	7
LW12	$\ln(W) \sim a_{sp} + a_{DD} + b_{sp} \ln(SL)$	7	8.3	4.7	0.020	13
LW13	$\ln(W) \sim a_{ss} + a_{DD} + b \ln(SL)$	8	9.8	3.9	0.030	12
LW14	$\ln(W) \sim a_{ss} + a_{DD} + b_{sp} \ln(SL)$	9	9.8	6.0	0.011	16
LW15	$\ln(W) \sim a_{exp} + a_{DD} + b \ln(SL)$	6	2.2	14.9	$< 10^{-3}$	19
LW16	$\ln(W) \sim a_{exp} + a_{DD} + b_{sp} \ln(SL)$	10	11.1	5.5	0.013	14
LW17	$\boldsymbol{\ln(W) \sim a_{exp} + a_{sp} + b \ln(SL)}$	**6**	**9.6**	**0**	**0.207**	**1**
LW18	$\boldsymbol{\ln(W) \sim a_{exp} + a_{sp} + b_{sp} \ln(SL)}$	***7***	***9.8***	***1.8***	***0.084***	***5***
LW19	$\boldsymbol{\ln(W) \sim a_{exp} + a_{ss} + b \ln(SL)}$	***8***	***11.0***	***1.4***	***0.101***	***3***
LW20	$\ln(W) \sim a_{exp} + a_{ss} + b_{sp} \ln(SL)$	9	11.0	3.4	0.037	9

the non-independent values in the two-species treatment. Generalised linear models (GLMs, Gamma distribution for biomass density and negative binomial distribution for population size) were used to analyse differences in final fish assemblage between treatments. To account for density-dependent effects, we included the initial biomass density TW_{ini} (g.m^{-3}) as a possible predictor in the analyses of population- and assemblage-level responses. Finally, we used linear regression to identify possible treatment differences in initial biomass densities $TW_{SS,\text{ ini}}$ and TW_{ini}.

We could not distinguish between the relative contribution of reproduction, survival and individual growth to population growth because we could not track the individuals in the experiments due to their minute size and susceptibility to handling and eventual tagging methods. Thus, to quantify potential effects of intra- and interspecific treatment on population growth, we instead quantified the (hypothetical) annualised, species-specific biomass-based growth rate as:

$$r_{SS} = \frac{1}{T} \ln \left(\frac{TW_{SS,\text{end}}}{TW_{SS,\text{ini}}} \right) \quad (2)$$

where $T = 0.3589$ years (131 days) is the duration of each experiment. We analysed r_{SS} using linear mixed-effect models (LMMs) with treatment-specific dispersion

and random intercept. We report the analyses of population- and assemblage-level responses only for the experiment in small mesocosms. The data from the large mesocosms were too limited for meaningful analyses and we comment only on the raw data from this experiment.

We used model selection to identify the most parsimonious (hereafter 'best') model with the lowest corrected Akaike Information Criterion (AICc) and other plausible models (ΔAICc ≤ 2) in each analysis (Burnham and Anderson 2002). The candidate model set included 20 models in the length-weight allometry analysis (LW1–LW20, Table 1), only the constant model and the model with the treatment effect in the analysis of initial total biomass density (iTW1 and iTW2) and species-specific biomass-based growth rate (ssr1 and ssr2) and five models including the full model with the statistical interaction between treatment and initial biomass density and all possible submodels being amongst the candidate models of final biomass density (species-specific: ssTW1–ssTW5, total: TW1–TW5) and population density (species-specific: ssTN1–ssTN5, total: TN1–TN5; Table 3).

We used the package 'glmmTMB' (Brooks et al. 2017) to implement the models and the package 'DHARMa' (Hartig 2020) to examine the model residuals; the 'nbinom1' link function was used in the negative binomial GL(M)M models. We reported the model parameter estimates with their 95% confidence intervals calculated with the 'sjPlot' package (Lüdecke et al. 2020) and visualised the model fits with the 'ggeffects' package (Lüdecke 2018). We classified the differences between groups as 'significant' if their 95% confidence intervals did not overlap, the length-weight allometry as significantly different from isometry if the 95% confidence interval of the allometric slope did not contain the value 3 and the population growth rate as significantly positive if its 95% confidence interval did not contain zero.

Results

In total, 4,348 fish individuals were collected from both small and large mesocosms at the end of the experiment. Both species responded differently to syntopy. While the single-species treatment contained on average 67 ± 66 (mean ± SD) individuals of sunbleak in small mesocosms and 408 ± 107 in large mesocosms, the syntopy treatment contained only 11 ± 12 and 18 ± 20 individuals, respectively. In contrast, the final topmouth gudgeon abundance was similar in both treatments in each experiment, with 54 ± 35 and 480 ± 98 individuals in the single-species treatment and 42 ± 29 and 279 ± 157 individuals in syntopy. No obvious mortality of sunbleak was observed during regular checks of mesocosms and 20 sunbleak kept alive in aquarium after the syntopy treatments survived two-month period without any disease symptoms.

Genetic verification of *Sphaerothecum destruens*

All samples were run with positive and negative controls and all reactions, except the positive control, were found negative, i.e. without the confirmed presence of *Sphaerothecum destruens* DNA (Suppl. material 1: fig. S1).

Individual-level response

Individual fish of both species differed greatly in body length and weight at the end of the experiment and the individually measured fish in all treatments clearly

included both the introduced individuals and their offspring in both experiments. Model selection identified five plausible models for the underlying length-weight allometries (Table 1). The best model (LW17) included a common allometric slope, but the intercept differed between species and experiments: the model predicted that topmouth gudgeon individuals were significantly heavier than sunbleak individuals of the same length from the same mesocosm volume and that individuals of the same species and length were significantly heavier in the large mesocosms than in the small ones. The magnitude of the latter effect was about two-thirds of the effect of species identity (Table 2 and Fig. 1). Three of the four other plausible models (LW101, LW18 and LW19) included a qualitatively equal effect of mesocosm volume, two models (LW3 and LW18) included a qualitatively equal effect of species identity and one plausible model (LW19) included a combined effect of species identity and syntopy, suggesting that sunbleak from the syntopy treatment tended to have a slightly lower weight than sunbleak from the single-species treatment and any topmouth gudgeon of the same length from the same mesocosm volume (Table 2).

Two of the other four models (LW10 and LW18) also included species-specific allometric slopes, but the differences between species were small and reversed between the two models. Allometric slope estimates in all five parsimonious models were slightly, but not significantly, lower than 3, i.e. consistent with an isometric or near-isometric growth of both species (Table 2). Importantly, we found no effect of population density on length-weight allometry and the effects of species identity and mesocosm volume were small (Fig. 1).

Table 2. Best model (LW17) and the other plausible models (LW10, LW19, LW3, LW18) of the length-weight allometries of both species. Parameter estimates given on the predictor scale as mean with 95% confidence intervals in parentheses. Predictors: intercept corresponds to a hypothetical sunbleak *Leucaspius delineatus* individual with *SL* = 1 mm from a large mesocosm and sunbleak-only treatment (LN); b = allometric slope, b_L = sunbleak allometric slope, b_P = topmouth gudgeon *Pseudorasbora parva* allometric slope, *species* = species-specific difference in intercept, *Experiment* = difference in intercept between mesocosm volumes, *SS* = differences in intercept between combined species and syntopy categories (see Materials and methods for details). Random effects: σ^2 = residual variance; τ_{00} = random effect variance; ICC = intra-class correlation; number of replicates N_{tank} = 32 and number of individuals N_{tot} = 448 for all models. R^2_m = marginal R^2, R^2_c= conditional R^2.

Predictors	LW17	LW10	LW19	LW3	LW18
(Intercept)	-11.1 (-11.4 to -10.8)	-11.0 (-11.3 to -10.7)	-11.0 (-11.3 to -10.7)	-11.1 (-11.4 to -10.8)	-11.2 (-11.6 to -10.7)
b	2.96 (2.88–3.04)	-	2.95 (2.87–3.04)	2.95 (2.87–3.03)	-
b_L	-	2.95 (2.86–3.03)	-	-	2.98 (2.86–3.10)
b_P	-	2.97 (2.89–3.06)	-	-	2.94 (2.83–3.05)
Species (*Pseudorasbora* vs. *Leucaspius*)	0.106 (0.052–0.159)	-	-	0.110 (0.055 – 0.165)	0.264 (-0.332–0.860)
Experiment (small vs. large)	-0.073 (-0.144 to -0.002)	-0.073 (-0.144 to -0.001)	-0.077 (-0.147 to -0.007)	-	-0.074 (-0.145 to -0.003)
SS (LY vs. LN)	-	-	-0.074 (-0.162–0.014)	-	-
SS (PN vs. LN)	-	-	0.068 (-0.015–0.152)	-	-
SS (PY vs. LN)	-	-	0.059 (-0.025–0.143)	-	-
Random effects					
σ^2	0.05	0.05	0.05	0.05	0.05
$\tau_{00,tank}$	0.00	0.00	0.00	0.01	0.00
ICC	0.08	0.08	0.07	0.10	0.08
R_m^2 / R_c^2	0.925 / 0.931	0.925 / 0.931	0.926 / 0.932	0.925 / 0.932	0.925 / 0.931

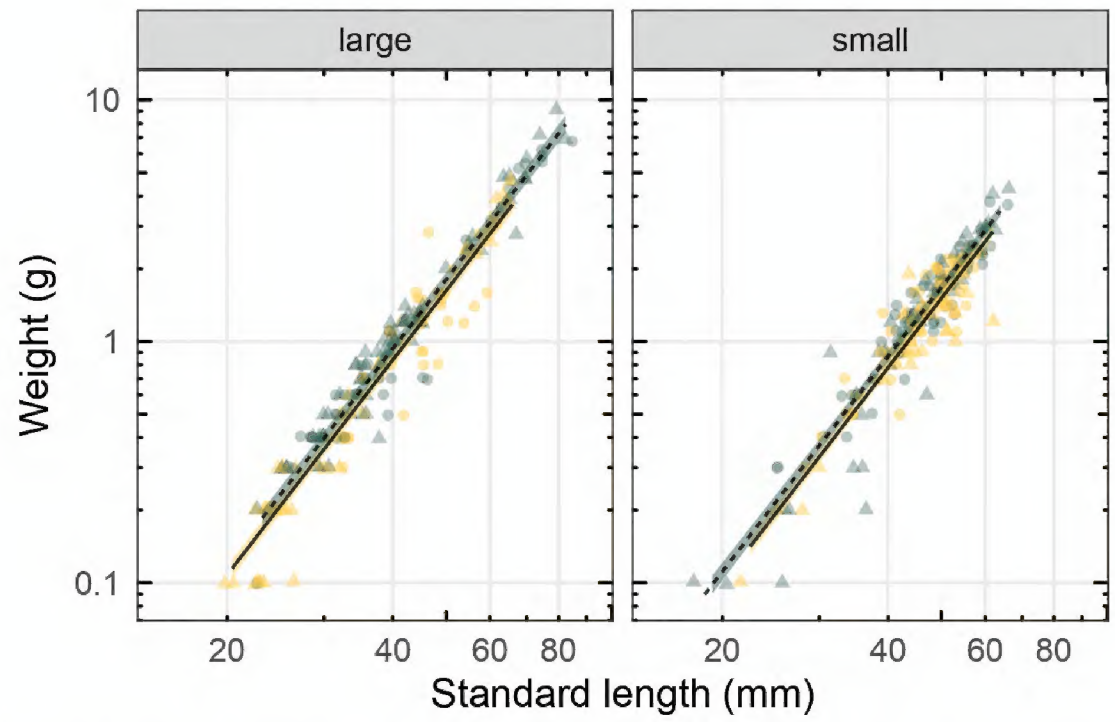


Figure 1. Predictions of the best model of the length-weight allometry of each species in the large (left panel) and small (right panel) mesocosms. Predictions (lines) shown with 95% confidence intervals (ribbons),based on the fixed effects; individual observations shown as symbols. Circles = single-species treatments, triangles = syntopy treatment. Yellow symbols and solid lines = sunbleak *Leucaspius delineatus*, dark green symbols and dashed lines = topmouth gudgeon *Pseudorasbora parva*.

Population- and assemblage-level responses

Final biomass and population densities varied amongst treatments, species and replicates in both mesocosm types. The sunbleak populations responded strongly to the presence of topmouth gudgeon in both mesocosm types (Suppl. material 1: figs S2, S3). Despite the relatively narrow range of initial population biomass, we also observed negative density-dependent growth in both mesocosm types. According to the best model, the final biomass density of sunbleak in the sunbleak-only treatment decreased significantly with initial biomass density in the small mesocosms, while the final biomass density of the other combinations of treatment and mesocosm type tended to increase with initial biomass density (Fig. 2a, Tables 3, 4). The predicted final biomass density of sunbleak was almost always significantly higher in the sunbleak-only treatment than in the syntopy treatment when the initial total biomass density was taken into account, while the predicted final biomass densities of topmouth gudgeon were similar in both treatments and always significantly higher than that of sunbleak in the syntopy treatment. The best model of final population density included only a strong negative density dependence and no differences between treatments (Fig. 2b), while the second plausible model also included differences between species and treatments and suggested the highest population densities of sunbleak and topmouth gudgeon in the single-species treatment, followed by topmouth gudgeon in the syntopy treatment and the lowest population densities of sunbleak in the syntopy treatment analogous to the biomass density responses (Tables 3, 4).

The best models for final total biomass and population densities in the small mesocosms included a statistical interaction between treatment and initial biomass density and other models were identified as plausible (Table 1). Observed and predicted final (biomass) densities were comparable on average across treatments in each experiment and were most sensitive to initial biomass density in the sunbleak-only treatment (Suppl. material 1: fig. S4, table S4).

Differences in the final population state between species and treatments were reflected in the biomass-based population growth rates. In the small mesocosms, the best model again included the statistical interaction between species and treatment

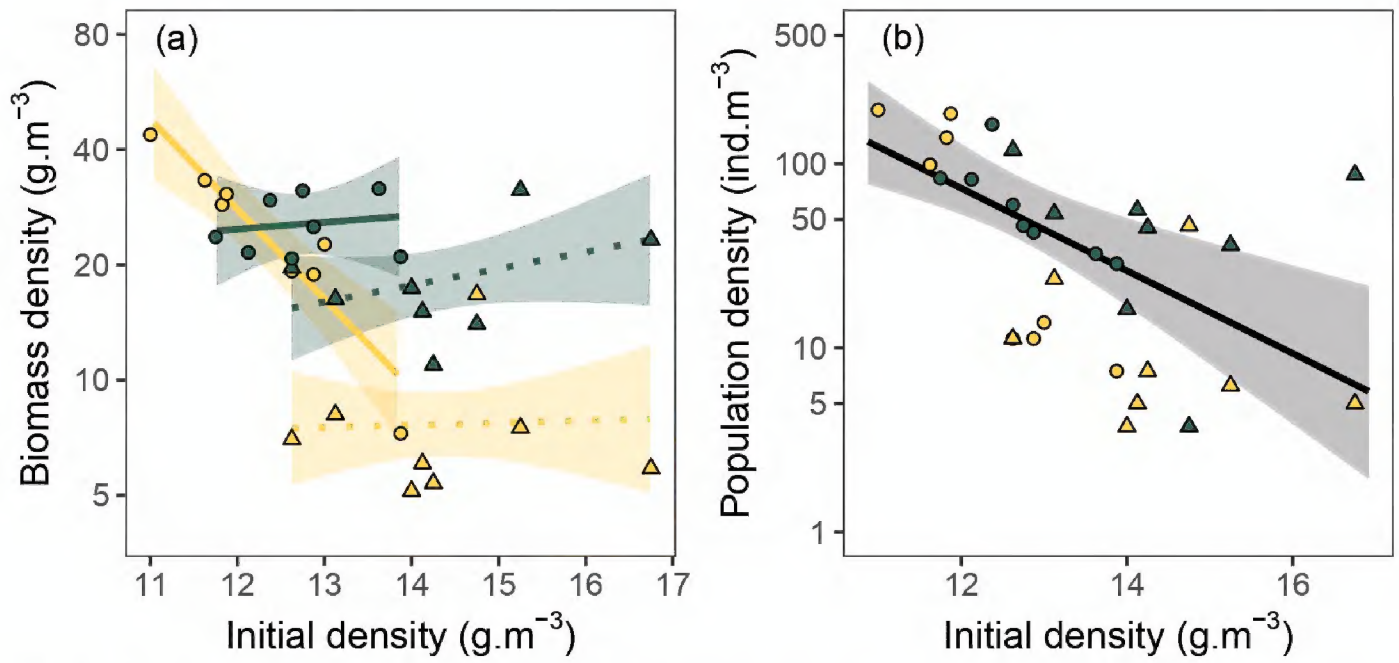


Figure 2. Predictions of the best models of the final biomass density (**a**) and final population density (**b**) of each species in the small mesocosms. Predictions shown as predicted values (lines) with 95% confidence intervals (ribbons), based on the fixed effects; individual observations shown as filled symbols. Filled circles and solid lines = single-species treatments, filled triangles and dotted lines = syntopy treatment. Colour: yellow = sunbleak *Leucaspius delineatus*, dark green = topmouth gudgeon *Pseudorasbora parva*, black and grey = no difference between species or treatments.

Table 3. Comparison of all candidate models of final population state (biomass density: TW_{ss}, population density: TN_{ss}) and biomass-based population growth rate (r) of each species and final state of the assemblage (biomass density: TW, population density: TN) in small mesocosms. Best model for each response variable in bold; other plausible models with ΔAICc ≤ 2 for each response variable highlighted in bold italics. Model structure: *SS* = combination of species identity and syntopy, *Trt* = treatment (sunbleak *Leucaspius delineatus*-only, topmouth gudgeon *Pseudorasbora parva*-only and syntopy), TW_{ini} = initial biomass density; models of species-specific final population states contain random effect component (1 | *Tank*); only the conditional model structure shown.

Response	Model	Model structure	df	ln(*L*)	ΔAICc	*w*	Rank
TW_{ss}	ssTW1	~ const.	3	-117.8	26.2	$< 10^{-3}$	5
	ssTW2	~ *SS*	6	-101.6	2.4	0.216	2
	ssTW3	~ TW_{ini}	4	-114.2	21.7	$< 10^{-3}$	4
	ssTW4	~ *SS* + TW_{ini}	7	-101.5	5.4	0.049	3
	ssTW5	**~ *SS* × TW_{ini}**	**10**	**-92.9**	**0**	**0.735**	**1**
TN_{ss}	ssTN1	~ const.	3	-152.9	11.8	0.002	5
	ssTN2	~ *SS*	6	-148.4	11.3	0.002	4
	ssTN3	**~ TW_{ini}**	**4**	**-145.7**	**0**	**0.576**	**1**
	ssTN4	***~ SS + TW_{ini}***	***7***	***-142.0***	***1.8***	***0.232***	***2***
	ssTN5	~ *SS* × TW_{ini}	10	-136.3	2.2	0.189	3
r	ssr1	~ const.	6	-49.9	5.8	0.052	2
	ssr2	**~ *SS***	**9**	**-41.6**	**0**	**0.948**	**1**
TW	TW1	~ const.	2	-83.6	8.7	0.013	2
	TW2	~ *Trt*	4	-83.6	14.2	0.001	4
	TW3	~ TW_{ini}	3	-83.4	10.9	0.004	3
	TW4	~ *Trt* + TW_{ini}	5	-82.9	16.1	$< 10^{-3}$	5
	TW5	**~ *Trt* × TW_{ini}**	**7**	**-71.0**	**0**	**0.982**	**1**
TN	TN1	~ const.	2	-120.0	8.7	0.011	4
	TN2	~ *Trt*	4	-119.7	13.5	0.001	5
	TN3	~ TW_{ini}	3	-117.5	6.2	0.038	3
	TN4	~ *Trt* + TW_{ini}	5	-113.5	4.5	0.091	2
	TN5	**~ *Trt* × TW_{ini}**	**7**	**-107.4**	**0**	**0.859**	**1**

Table 4. Best models (ssTW5, ssTN3, ssr2, TW5 and TN5) and the other plausible model (ssTN4) of the final population density, biomass density and population growth rates of both species (ssTW5, ssTN3, ssTN4, ssr2) and the whole fish assemblage (TW5, TN5) in small mesocosms. Predictors: intercept corresponds to a mesocosm in sunbleak *Leucaspius delineatus*-only treatment (LN) with TW_{ini} = 12.3 g.m^{-3}; *SS* = effect of species and syntopy treatment relative to the LN treatment; *DD* = slope of the density-dependent effect (i.e. change per unit of total initial biomass TW_{ini}); DD_{SS} = slope of the treatment specific density-dependent effect (LN treatment) or the slope difference relative to the LN treatment. Parameter estimates given on the predictor scale as mean with 95% confidence intervals in parentheses. N_{tank} = 24 for all five models and number of populations N_{pop} = 32 for models ssTW5, ssTN3, ssTN4 and ssr2. R_2 value for TW5 = Nagelkerke R_2, R_2 value for TN5 = Mc-Fadden's R_2. Other symbols as in Table 2.

Predictors	ssTW5	ssTN3	ssTN4	ssr2	TW5	TN5
(Intercept)	3.15 (2.96–3.33)	3.55 (3.23–3.87)	3.98 (3.61–4.34)	1.73 (0.62 – 2.84)	3.15 (3.02–3.28)	3.75 (3.37–4.12)
SS (LY vs. LN)	-1.11 (-1.38 to -0.85)	-	-1.50 (-2.27 to -0.74)	-1.79 (-3.10 – -0.47)	-	-
SS (PN vs. LN)	0.09 (-0.17–0.35)	-	0.02 (-0.49–0.54)	0.17 (-0.99 – 1.33)	0.09 (-0.09 – 0.28)	0.21 (-0.28 – 0.70)
SS (PY vs. LN)	-0.24 (-0.50–0.02)	-	-0.52 (-1.12–0.08)	0.84 (-0.40 – 2.09)	-	-
SS (syntopy vs. LN)	-	-	-	-	0.11 (-0.07 – 0.30)	0.21 (-0.28 – 0.69)
DD	-	-0.52 (-0.76 to -0.27)	-0.59 (-0.88 to -0.30)	n.a.	-	-
DD_{SS} (LN)	-0.54 (-0.77 to -0.31)	-	-	n.a	-0.54 (-0.70 to -0.38)	-1.14 (-1.52 to -0.77)
DD_{SS} (LY vs. LN)	0.55 (0.28–0.83)	-	-	n.a	-	-
DD_{SS} (PN vs. LN)	0.58 (0.22–0.94)	-	-	n.a	0.58 (0.32–0.84)	0.60 (-0.00–1.20)
DD_{SS} (PY vs. LN)	0.64 (0.37–0.91)	-	-	n.a	-	-
DD_{SS} (syntopy vs. LN)	-	-	-	n.a.	0.62 (0.42–0.81)	1.06 (0.54–1.57)
Variance						
(Intercept)	-	-	-	0.47 (-0.02–0.96)	-	-
SS (LY vs. LN)	-	-	-	-0.46 (-1.15–0.24)	-	-
SS (PN vs. LN)	-	-	-	-1.24 (-1.93 to -0.54)	-	-
SS (PY vs. LN)	-	-	-	-0.68 (-1.37–0.01)	-	-
Random effects						
σ^2	0.06	0.08	0.00	(1.61, 0.47, 1.02, 0.82)	n.a.	n.a.
$\tau_{00,tank}$	0.00	0.00	0.00	0.00	n.a.	n.a.
ICC	0.06	0.00	0.00	(0.00, 0.00, 0.00, 0.00)	n.a.	n.a.
R_m^2 / R_c^2	0.811 / 0.824	0.889 / 0.889	0.907 / 0.907		0.656	0.105

and predicted significantly positive population growth rates of sunbleak in the single-species treatment and of topmouth gudgeon in both treatments and a zero growth rate of sunbleak in the syntopy treatment (Fig. 3, Tables 3, 4). The relative response of population growth rates to the syntopy treatment tended to be positive for topmouth gudgeon and significantly negative for sunbleak and the estimated variance of population growth rate was highest in the sunbleak-only treatment, intermediate for both species in the syntopy treatment and lowest in the topmouth gudgeon-only treatment (Fig. 3 and Table 4). We observed the same relative response of population growth rates of both species to syntopy in the large mesocosms despite higher absolute values of population growth rates and lower final population densities than in the small mesocosms (see Suppl. material 1: fig. S3).

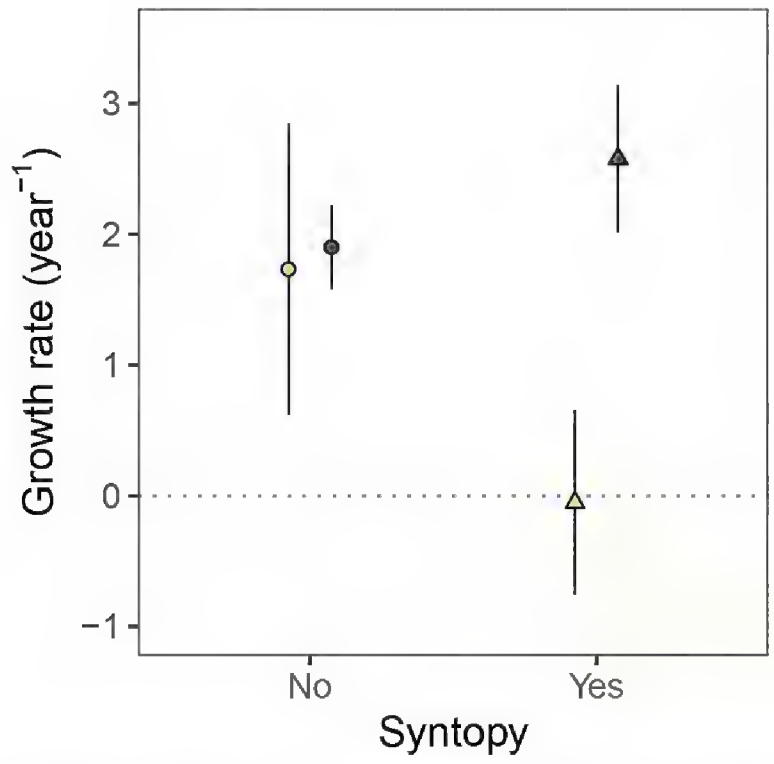


Figure 3. Predictions of the best model (mean with 95% confidence interval) of biomass-based population growth rate of each species in each syntopy treatment in the small mesocosms. Filled circles = single-species treatments, filled triangles = syntopy treatment. Colour: yellow = sunbleak *Leucaspius delineatus*, dark green = topmouth gudgeon *Pseudorasbora parva*.

Discussion

This study provides evidence that competition with topmouth gudgeon negatively impacts sunbleak populations through direct or indirect trophic interactions. The invasive topmouth gudgeon is an aggressive species that can utilise various food sources and even harm other fish species at high densities by eating their mucus and skin (Oberle et al. 2019). Its batch spawning leads to the production of many cohorts within a year and to rapid saturation and depletion of the ecosystem (Gozlan et al. 2010; Adámek et al. 2024). The effects of topmouth gudgeon on the ecosystem are particularly visible in the depletion of large zooplankton, which impacts the growth of other fish (Musil et al. 2014; Kajgrová et al. 2022). However, sunbleak possesses similar life history characteristics, such as batch spawning, rapid maturation, rapid population growth and the ability to reach high population densities (Gozlan et al. 2003; Pinder and Gozlan 2004; Interesova 2012). Therefore, the observed outcome of interspecific competition between the two species combined with similar population growth of both species in the single-species treatments in our mesocosm experiments demonstrates that topmouth gudgeon is competitively superior to sunbleak.

Topmouth gudgeon impact on sunbleak: evidence of intra- and interspecific competition

We found a significantly negative impact of topmouth gudgeon on sunbleak population growth rate and final biomass despite no identifiable effect on sunbleak individuals and an ambiguous effect on final sunbleak population density (i.e. the effect of treatment was excluded from the most parsimonious model, but retained in the other plausible model). This seemingly inconsistent effect on the different measures of sunbleak population-level response points towards differences in the size structure of the sunbleak or topmouth gudgeon populations and their dependence on initial biomass density in both treatments. We cannot resolve this issue as it was not logistically possible to reliably measure all individuals at the end of the experiment, as sunbleak is a fragile species and surviving individuals were stocked

back to breeding ponds. Interestingly, the biomass-based population growth rate of topmouth gudgeon was slightly higher in syntopy than in the single-species treatment, indicating that topmouth gudgeon faces stronger intraspecific competition than interspecific competition from sunbleak. Moreover, the combined final biomass of both species in the syntopy treatment did not differ from the final biomass of each species in the single-species treatment, suggesting a symmetry between the population-level gains of topmouth gudgeon and losses of sunbleak.

Both sunbleak and topmouth gudgeon demonstrated high population growth rates in the single-species treatments reaching similar final densities and biomasses, which is consistent with the ecology of both species (Farr-Cox et al. 1996; Gozlan et al. 2003, 2010). Sunbleak populations in the small mesocosms were also more unstable, having higher variance in population growth in the single-species treatment. This could be due to higher sensitivity of sunbleak to the experimental conditions, whereby, for example, the higher temperature tolerance of topmouth gudgeon compared to the sunbleak could play a role (Radtke et al. 2022). The observed instability is consistent with data on wild sunbleak populations, where some populations fail to establish for unknown reasons (Farr-Cox et al. 1996). The instability may also indicate that caution should be exercised when drawing conclusions about the ecology of sunbleak populations, based on manipulative experiments.

In this study, an individual marking technique such as PIT tagging in the body cavity (Šmejkal et al. 2019) would help to determine the growth of the parent fish stocked in mesocosms, but this was not possible due to the small size of the species studied and the sensitivity of the sunbleak to handling. This would also help to assess individual growth rates for both species in the syntopic and single species treatments. Therefore, the study focused instead on the growth rates of the populations.

Populations of both species in small and large mesocosms showed a similar qualitative response to syntopy, but the results suggested some differences between both mesocosm types. Large mesocosms had higher absolute values of population growth rates and lower final population densities, suggesting that populations in large mesocosms were probably not yet affected by strong density-dependent effects. Large mesocosms probably also provided a better habitat for the species and allowed faster growth rates, as they better represented small floodplain pools, the natural habitat of sunbleak (Farr-Cox et al. 1996; Interesova 2012; Šmejkal et al. 2025). Consistent with the better conditions in large mesocosms compared to small mesocosms was also the length-weight allometries, where individuals of both species from large mesocosms were heavier than same-sized individuals from small mesocosms. These results suggest the importance of habitat structure and waterbody size in mediating competitive interactions, with small or simplified environments amplifying the effects of interspecific pressures on recruitment and biomass accumulation.

Quite unexpectedly, despite the low range of initial population biomass, we also observed negative density-dependent growth of sunbleak in the small mesocosms. This could be an indication of over-compensatory effects or unstable population dynamics, for example, due to asymmetric competition between adults and juveniles or cannibalistic interactions. The latter is quite likely, as the space was limited and sunbleak has a relatively large gape size compared to its body size (Interesova 2012).

While we have shown the impact of topmouth gudgeon on the final biomass density of the sunbleak in our experimental set-up, we have not identified the exact mechanism behind the low population growth rate in the presence of topmouth gudgeon. One of the possibilities is spawning interference. Gozlan and

Beyer (2006) have shown that hybridisation can be induced in the laboratory, but this resulted in hybrids that died at the first larval stage. In our study, no suspected hybrids were identified during species sorting, but this does not rule out the possibility that reproduction of sunbleak was slowed by hybridisation and subsequent mortality of hybrids. Further research is needed to verify this possibility.

Sunbleak declines: the role of rosette agent

Topmouth gudgeon individuals can carry the rosette agent, an intracellular eukaryotic organism, which is partly responsible for the negative effects of topmouth gudgeon on the native fish fauna (Andreou and Gozlan 2016). This disease can affect various fish species, from salmonids to common bream (*Abramis brama*) and other cyprinids (Paley et al. 2012; Al-Shorbaji et al. 2015). In an experiment conducted with sunbleak in the laboratory and in a pond, Gozlan et al. (2005) demonstrated a complete inhibition of sunbleak reproduction in direct association with topmouth gudgeon, an asymptomatic carrier of the disease. In the laboratory experiment, this inhibition was caused exclusively by the water pumped from topmouth gudgeon tanks, without any direct contact between the two species. Furthermore, this experiment was associated with ~ 70% sunbleak mortality in the laboratory (Gozlan et al. 2005).

In our experiment, topmouth gudgeon outperformed the sunbleak in the population growth rate to a similar extent as in the pond experiment of Gozlan et al. (2005), in which topmouth gudgeon carried the disease. Contrary to their findings, we found no infected sunbleak individuals during our experiment and in sunbleak held in aquaria after syntopy and they spawned successfully in the syntopic treatments. Moreover, Spikmans et al. (2013) found that the prevalence of the rosette agent in topmouth gudgeon is not absolute and the disease has not yet been detected in Czechia (M. Palíková, pers.comm).

Taken together, this suggests that the impacts of topmouth gudgeon on sunbleak and more generally on the native fish fauna are more diverse and not limited to the spread of a novel disease. Future research should explore the topmouth gudgeon competitive and predation effects on sunbleak and other native fish species in more detail.

Impacts of invasions on native fishes

Invasions are a leading cause of fish extinctions, many of which are due to interspecific competition (Clavero and García-Berthou 2005; Strayer 2010). This study provides a limited, but important evidence from mesocosm experiments in which niches are likely to be less differentiated than in a more complex environment. However, the decline of the sunbleak in its native range and its shift to endangered categories in many EU countries suggests that the impact of topmouth gudgeon is significant even in pristine wetlands and other waterbodies (Šmejkal et al. 2025). A recent survey of small waterbodies in Czechia, which used to be frequently inhabited by sunbleak in the past, found eight times more localities of invasive topmouth gudgeon than of native sunbleak and both species occurred in syntopy at only one site (Thomas et al. 2024). In contrast to that, no decline of sunbleak has been observed in the large Lake Grand-Lieu (Carpentier et al. 2008). It remains to be investigated how the complexity and the size of the waterbody influence the competition between the two species. The interplay between invasive species pressure and habitat degradation may be particularly detrimental for species with

narrow ecological niches, such as the sunbleak (Šmejkal et al. 2025). Conservation strategies should, thus, integrate both invasive species management and habitat restoration to sustain viable populations.

Wetland fish specialists and their gradual decline in Anthropocene

The intensive use of land for agriculture and the alteration of rivers are leading to an extreme loss of wetlands and the natural flow regime associated with the function of wetlands (Arthington 2012; Grill et al. 2019). The remaining wetlands, serving as primary refugia for wetland-specialised fish species, are increasingly invaded by invasive species (Šmejkal et al. 2025). The sunbleak is an example of fast declining species that originally thrived in wetlands, with secondary habitat in abandoned ponds and flooded stone quarries (Thomas et al. 2024). A similar example is the competitive exclusion of the crucian carp (*Carassius carassius*) by the invasive gibel carp (*C. gibelio*) and topmouth gudgeon (Tapkir et al. 2022; Šmejkal et al. 2024a, b), whose populations are also scarce and mostly occur in secondary habitats (Thomas et al. 2025). It seems crucial to find management strategies for the conservation of these two native wetland fish species, as well as to species with similar population trends.

Conclusion and future directions

This study shows that the direct and indirect trophic interactions with topmouth gudgeon can have a detrimental effect on sunbleak populations. The underlying mechanisms could include exploitative competition and higher effectiveness of resource utilisation in topmouth gudgeon or its intra-guild predation on the eggs, larvae and/or juveniles of sunbleak. Future experiments should explore the interactions between the different size classes of both species in detail.

Species co-existence and competitive exclusion are also affected by habitat productivity and temperature: successful invasions, often leading to the loss of the native species, are more likely in warm, productive habitats that are becoming more common with the ongoing climate change (Dijoux et al. 2024). We did not vary temperature or nutrient input in our experiments; future studies should explore the role of warming and eutrophication on the competition between native and invasive species such as topmouth gudgeon and sunbleak.

Sunbleak and topmouth gudgeon occasionally co-exist, especially in larger ecosystems with more diverse communities (Carpentier et al. 2008). This calls for more detailed studies of the possible role of niche divergence in larger ecosystems and top-down control of invasive species by piscivorous fish.

Sunbleak populations undergo serious population decline in their European distribution range. Thus, from a conservation perspective, sunbleak populations should be managed and kept outside the areas invaded by topmouth gudgeon using species translocations, at least in the countries with the fastest population declines.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

The field sampling and experimental protocols used in this study were performed under the guidelines and permission from the Experimental Animal Welfare Commission under the Ministry of Environment of the Czech Republic (MZP/2024/630/2999). Fish were kept under the permission of the Ministry of Agriculture (ref. no. MZE-22409/2024-13143).

Use of AI

No use of AI was reported.

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Author contributions

MŠ, AR, KT, PAG, SRT, YS, FL and MB conducted the experiments; MŠ and KT designed the study; AR and MŠ prepared data for the analysis; DB and MŠ conducted the data analysis; MB Conducted genetic analysis; MŠ and DB wrote the first draft. All authors contributed substantial feedback during manuscript preparation.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary tables and figures

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Data type: docx

Explanation note: **table S1.** Comparison of all candidate models of the total biomass density at the start of each mesocosm experiment. **fig. S1.** All samples were without the confirmed presence of *Sphaerothecum destruens* DNA (L = ladder; PC = positive control; NC = negative control; topmouth gudgeon *Pseudorasbora parva* alone = 1-2, 47-54; topmouth gudgeon syntopy = 3-12; sunbleak *Leucaspius delineatus* alone = 13-22; sunbleak syntopy = 23-46). **fig. S2.** Total biomass density (top row) and population density (bottom row) in individual tanks at the start and end of each mesocosm experiment. **fig. S3.** Total biomass density (top row) and population density (bottom row) of each species in individual tanks at the start and end of each mesocosm experiment. **fig. S4.** Predictions of the most parsimonious model of final biomass density (a) and final population density (b) of both species combined in the small mesocosms.

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